

# Host-Plant Effects on the Efficacy of Two Predators Attacking Russian Wheat Aphids (Homoptera: Aphididae)

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**ABSTRACT** We compared the effectiveness of generalist predators in reducing populations of the Russian wheat aphid, *Diuraphis noxia* (Mordvilko), on range grasses that differ in leaf architecture. Crested wheatgrass, *Agropyron desertorum*, produces relatively broad leaves and, like wheat, provides aphids with rolled leaves as potential refuges from natural enemies; Indian ricegrass, *Oryzopsis hymenoides*, bears linear, involute leaves that are usually too narrow to permit aphid aggregations within leaf rolls. We established aphid populations on each host and then introduced either neonate larvae of the lacewing *Chrysoperla plorabunda* (Fitch) or adults of the ladybird beetle *Propylea quatuordecimpunctata* L. On seedlings, there was an interaction between the effects of predator species and host-plant species; beetles were less effective on crested wheatgrass than on Indian ricegrass, but lacewings eliminated or nearly eliminated aphid populations on both hosts. On whole plants in the field, both predators tended to be more effective on Indian ricegrass than on crested wheatgrass. In all experiments, lacewing larvae were superior to beetles in causing extinction of aphid populations. These results are consistent with behavioral observations of foraging predators, and suggest that the host-plant effects on the 3rd trophic level can depend on predator species as well as plant stage.

**KEY WORDS** *Diuraphis noxia*, tri-trophic interactions, ladybird beetle, lacewing, biological control

SEVERAL PLANT TRAITS can influence the ability of natural enemies to suppress populations of herbivorous insects (Price 1986, Barbosa and Letourneau 1988). Although most research has considered how plant secondary chemicals or specific morphological traits (such as trichome density) affect enemies, recent studies have emphasized the more subtle role of plant architecture (Kareiva and Sahakian 1990, Marquis and Whelan 1996). Architectural differences among plants can affect predation rates by modifying either the searching behavior of predators (Carter et al. 1984, Grevstad and Klepetka 1992) or the availability of spatial refuges for prey (Hawkins et al. 1993). In this study, we compared the effectiveness of 2 predators in reducing populations of the Russian wheat aphid, *Diuraphis noxia* (Mordvilko), on grasses that differ in leaf architecture.

The Russian wheat aphid attacks several species of perennial grasses in western North America (Kindler and Springer 1989, Clement et al. 1990, Armstrong et al. 1991). Two common, nutritionally suitable grasses in Utah are crested wheatgrass, *Agropyron desertorum* (Fischer ex Link) Schultes, and Indian ricegrass, *Oryzopsis hymenoides* (Roemer & Schultes) Ricker (Messina et al. 1993a).

We hypothesized that architectural differences between these hosts could affect the vulnerability of *D. noxia* to generalist predators (Messina et al. 1995). The Russian wheat aphid forms compact aggregations within immature, furled leaves or at the junctions of leaf blades and leaf sheaths (Burd and Burton 1992), and it has been suggested that feeding in such concealed sites protects the aphid from some natural enemies (Formusoh and Wilde 1993, Kauffman and LaRoche 1994). Whereas crested wheatgrass produces broad, flat leaves and open leaf rolls like those of wheat, Indian ricegrass bears filiform, involute leaves (i.e., leaves rolled inward so tightly that only the abaxial [lower] surface may be exposed [Stubbendieck et al. 1992]). Preliminary observations suggested that these differences affect the locations of aphids (see *Discussion*). Because any architectural effects on aphid susceptibility may depend on plant stage, we estimated predation rates on both seedlings and field plants of each grass species.

We examined host-plant effects on the susceptibility of *D. noxia* to the lacewing *Chrysoperla plorabunda* (Fitch) [also referred to as *C. carnea* (Stephens), cf., Tauber and Tauber 1987, Henry et al. 1993], and the ladybird beetle *Propylea quatuordecimpunctata* (L.). The beetle has been imported from Eurasia specifically for the suppression of *D. noxia*, but it has become established only in the northeastern United States (Michels and Flanders 1992, Obrycki et al. 1993). We chose neonate lacewing larvae

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and adult beetles to represent predators in different size classes (although the 2 species obviously differ in other traits). Neonate lacewing larvae are nearly as small as *D. noxia* adults (lacewing length  $\times$  maximum width  $\approx 2.0 \times 0.5$  mm; aphid length  $\times$  width  $\approx 1.5 \times 0.5$  mm) and are considerably smaller than beetle adults (beetle length  $\times$  width  $\approx 4.3 \times 3.3$  mm). Kauffman and LaRoche (1994) have suggested that adults of *P. quatuordecimpunctata* may be too large to gain access to aggregations of *D. noxia* in rolled leaves of wheat.

### Materials and Methods

**Insect Sources.** Russian wheat aphids were obtained from a laboratory colony maintained on 'Hansel' winter wheat, *Triticum aestivum* L. (Messina et al. 1993a, voucher specimens were deposited in the Utah State University Insect Collection). Lacewing larvae were obtained from eggs supplied by Rincon-Vitova Insectaries, Ventura, CA, and were used <16 h after egg hatch. Beetles were supplied by the USDA-APHIS National Biological Control Laboratory in Niles, MI. They were fed aphids ad libitum for 9 d and then starved for 16 h before they were used in the experiments. We did not distinguish the beetle sexes; differences in aphid consumption between males and females (e.g., Hemptinne et al. 1996) would merely increase variation within treatments and thus reduce our ability to detect host-plant effects.

**Greenhouse Experiment.** A greenhouse experiment examined predator effectiveness on grass seedlings. Seeds of 'Nordan' crested wheatgrass and 'Paloma' Indian ricegrass were germinated on blotter paper in the laboratory and individually transplanted into cylindrical pots (6.4 cm diameter by 25 cm high) containing a 3:1 mixture by volume of sand and peat moss. When plants bore 3–5 tillers, we placed cellulose-acetate cages (4.1 cm diameter by 32 cm high) over 70 plants per species. Organdy-cloth windows on the sides of cages provided ventilation. We used a camel's-hair brush to add 3 apterous, adult aphids per plant. After 14 d, we harvested 10 plants per species into 70% ethanol to estimate aphid densities at the time predators were added. The remaining 60 plants per species received 3 lacewing larvae, 1 beetle, or nothing (20 replicates per treatment). These plants were harvested 7 d after predators were introduced (21 d after aphids were added), and we recorded the number of aphids per plant as well as the presence of predators. In this experiment (and in those described below), virtually all plants bore at least 1 predator when they were harvested; lacewing larvae had progressed to the 2nd (middle) instar. Although a few adult beetles laid eggs, we never recovered beetle larvae in any experiment. Greenhouse temperatures varied in a daily, sinusoidal pattern between 15 and 25°C.

**Field Experiments.** We compared predation rates on field plants in 3 experiments in 1995 and 1996. A common garden containing 72 plants per grass spe-

cies was established in each year. Plants were grown in a greenhouse until they produced several tillers. In late April, we transplanted them into a plot at the Greenville Experimental Farm in North Logan, UT (Messina et al. 1993a). Plants were interspersed randomly in 12 contiguous blocks and spaced 1 m apart. Daily maximum and minimum temperatures during each field experiment were provided by the Utah Climate Center, which maintains a weather station at the site.

The 1995 experiment was conducted in July and August, when plants bore 15–30 tillers. We added 10 adult aphids to each of 72 caged plants (36 per species) on 26 July. Cages consisted of a cylinder of organdy cloth attached to a PVC ring surrounding the base of the plant, and were closed at the top with wire attached to a bamboo stake. On 9 August, each plant received 15 neonate lacewing larvae, 5 beetles, or nothing (12 replicates per treatment). We harvested all plants 8 d after we added predators (22 d after we added aphids). We used Berlese funnels under 40-W incandescent lights to extract aphids and predators into jars containing 70% ethanol.

A similar experiment was conducted earlier in the growing season in 1996. We added 12 aphids to each of 37 plants per species on 14 June, when plants bore 10–20 tillers. On 27 June, we harvested 7 plants per species to estimate aphid density at the time of predator introductions (this step was not taken in 1995). The remaining 30 plants received 20 lacewing larvae, 6 beetles, or nothing (10 replicates per treatment). We harvested these plants 11 d after predators were added (24 d after aphids were added) and again used Berlese funnels to collect predators and aphids.

A 3rd experiment used individual culms instead of whole plants. This experiment used flowering plants from the garden established in 1995. On 10 May 1996, we added 3 aphids to each of 84 caged plants (42 plants per species). Cages were similar to those used in the greenhouse. Each cage was positioned over the top 20 cm of 2 adjacent culms per plant and was supported by bamboo stakes and wire. Culms were inserted through a radial slit in a foam plug at the bottom of the cage. After 14 d, we harvested 6 plants per species to estimate aphid densities when predators were added. The remaining 36 plants per species received 4 lacewing larvae, 2 beetles, or nothing (12 replicates per treatment). We harvested these plants 11 d after predators were added. Most culms bore inflorescences by this date, so that any host-plant effect could depend on leaf structure, inflorescence structure, or both. Crested wheatgrass bears a spike inflorescence with dense, overlapping spikelets; Indian ricegrass produces a diffuse panicle with widely spaced branches (Stubbendieck et al. 1992).

**Leaf Measurements.** We measured leaf characteristics on field plants and seedlings. Culms without inflorescences were sampled randomly from the edges of mature plants in a common garden established in 1990 (Messina et al. 1993a). We measured

Table 1. Mean  $\pm$  SE number of aphids on greenhouse seedlings of 2 range grasses in the presence or absence of predators

Treatment	Crested wheatgrass	Indian ricegrass
Early harvest plants <sup>a</sup>	37.0 $\pm$ 6.3	34.1 $\pm$ 3.5
Experimental plants <sup>b</sup>		
Control	129.6 $\pm$ 25.8	128.9 $\pm$ 16.8
Lacewing larvae	6.8 $\pm$ 4.4	1.9 $\pm$ 0.7
Ladybird beetles	29.9 $\pm$ 13.7	5.7 $\pm$ 1.3

<sup>a</sup> Early harvest plants estimate aphid densities when predators were added;  $N$  = 10 plants per host.

<sup>b</sup>  $N$  = 20 plants per host.

culm height and the diameter of the newest leaf roll on 10 culms of crested wheatgrass and 8 culms of Indian ricegrass. On seedlings, we measured 3 traits on the newest unrolled leaf of 27 plants per species: leaf length, maximum width, and the width of the leaf-sheath/leaf-blade junction. The junction of the leaf sheath and leaf blade (Stubbendieck et al. 1992) is the typical feeding site for *D. noxia* on either rolled or unrolled leaves, and its width is proportional to leaf-roll diameter on rolled leaves.

**Data Analyses.** We used a 2-way analysis of variance (ANOVA) to examine the fixed effects of plant species (2 levels) and predator treatment (3 levels) on aphid density (Wilkinson et al. 1996). Densities were transformed as  $\log_{10}(N + 1)$  to increase homogeneity of variances. We discarded data from a few field plants (3 of 72 in 1995 and 1 of 60 and 2 of 72 in 1996) because other arthropod predators were found in the cages. *T*-tests compared leaf dimensions between grass species, as well as the densities of aphids (log-transformed) at the time predators were introduced into cages.

## Results

**Greenhouse Experiment.** Aphid densities were similar on seedlings of the 2 grasses at the time that predators were introduced (Table 1;  $t = 0.07$ ,  $df = 18$ ,  $P = 0.95$ ). By the end of the experiment, aphid densities on control plants had increased 40-fold

from an initial density of 3 aphids per plant. The introduction of predators substantially reduced aphid populations on both hosts (Table 1). In addition to a significant effect of predation, there was a marginally significant effect of host plant on final aphid density (Table 2). Because aphids were equally abundant on control plants of the 2 hosts, this host-plant effect was largely the result of the lower efficacy of predators on crested wheatgrass, particularly for ladybird beetles (Table 1). Lacewing larvae reduced mean aphid densities by 95% or more (relative to control plants) on both grasses; beetles reduced aphid densities by 96% on Indian ricegrass versus 76% on crested wheatgrass. The stronger effect of host plant on beetle predation than on lacewing predation led to a significant interaction between plant and predation treatments in the ANOVA (Table 2).

To compare the efficacy of the 2 predators directly, we also performed ANOVA with control plants deleted. The effect of predator treatment (i.e., lacewings versus beetles) remained highly significant ( $F = 27.03$ ;  $df = 1, 75$ ;  $P < 0.001$ ). The effect of host plant was also significant and reflects higher aphid densities on crested wheatgrass among plants receiving predators (Table 1;  $F = 8.25$ ;  $df = 1, 75$ ;  $P < 0.01$ ). The interaction between these treatments was marginally significant ( $F = 3.51$ ;  $df = 1, 75$ ;  $P = 0.06$ ), which again suggests a greater effect of plant species on the efficacy of beetles than on the efficacy of lacewing larvae.

The impact of predation can also be estimated by the probability of aphid extinction, which depended more on predator species than on plant species. Although mean aphid densities suggested that lacewing larvae were more effective on Indian ricegrass than on crested wheatgrass (Table 1), this predator eliminated all aphids from the same number of plants (10 of 20) of each host. In contrast, beetles eliminated aphids from only 3 Indian ricegrass plants and 1 crested wheatgrass plant. As expected, aphid colonies persisted on all control plants.

Table 2. Two-way ANOVA for the effects of plant species and predation treatment on aphid density in greenhouse and field experiments

Experiment	Source	df	F	P
Greenhouse experiment	Host plant	1	3.36	0.07
	Predation	2	143.93	<0.001
	Host plant $\times$ predation	2	4.90	<0.01
	Error	113		
1995—whole plants	Host plant	1	10.84	<0.01
	Predation	2	21.74	<0.001
	Host plant $\times$ predation	2	1.25	0.29
	Error	63		
1996—whole plants	Host plant	1	10.83	<0.01
	Predation	2	46.67	<0.001
	Host plant $\times$ predation	2	1.31	0.28
	Error	53		
1996—individual culms	Host plant	1	0.37	0.55
	Predation	2	68.75	<0.001
	Host plant $\times$ predation	2	1.38	0.26
	Error	64		

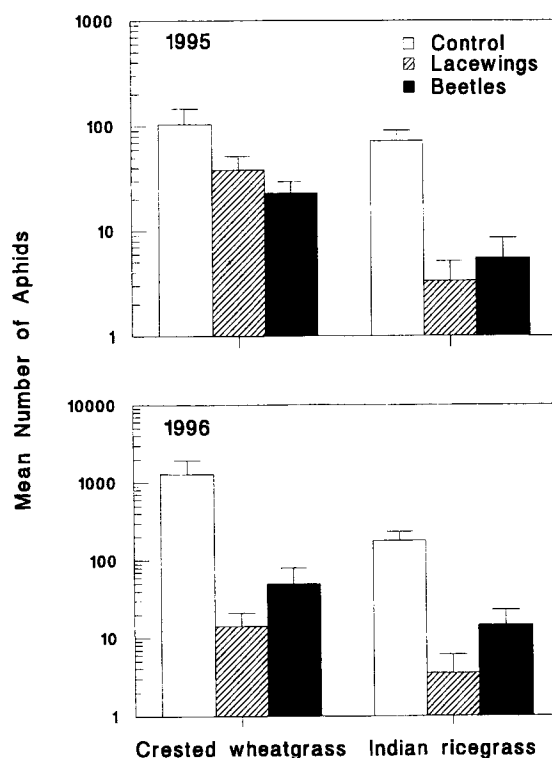


Fig. 1. Mean aphid densities  $\pm 1$  SE on whole plants of crested wheatgrass or Indian ricegrass with or without predators in 2 field experiments.  $n = 12$  plants per treatment in 1995 and 10 plants per treatment in 1996. Note the log scale on the ordinate.

**Field Experiments.** Aphid populations grew at a modest rate on control plants in 1995; mean aphid densities increased 10-fold on crested wheatgrass and 7-fold on Indian ricegrass from the initial density of 10 aphids per plant (Fig. 1). Final aphid densities depended on both host-plant and predation treatments, but, in contrast to the greenhouse experiment, there was no plant species  $\times$  predation interaction (Table 2). Both predators were less effective on crested wheatgrass than on Indian ricegrass. Lacewing larvae reduced mean aphid density by 95% on Indian ricegrass versus 63% on crested wheatgrass; beetles reduced aphid densities by 92 and 78% on the respective hosts (Fig. 1; note the use of a log scale because means differed by more than an order of magnitude). After control plants were removed from the analysis, predation treatment no longer had a significant effect on aphid density ( $F =$

0.10;  $df = 1, 44$ ;  $P = 0.75$ ), but the effect of host plant remained highly significant as a consequence of higher aphid densities on crested wheatgrass ( $F = 11.11$ ;  $df = 1, 44$ ;  $P < 0.01$ ). The interaction between host plant and predation treatments was again nonsignificant ( $F = 0.26$ ;  $df = 1, 44$ ;  $P = 0.61$ ), which means that the increase in effectiveness on Indian ricegrass was similar for the 2 predators. Lacewing larvae eliminated aphids from 7 of 12 Indian ricegrass plants and 3 of 12 crested wheatgrass plants. Beetles caused aphid extinctions on 4 Indian ricegrass plants and 2 crested wheatgrass plants.

The 1996 whole-plant experiment was complicated by a large difference in the number of aphids on control plants of the 2 hosts. At the time predators were added, mean  $\pm$  SE aphid density was already 34% higher on crested wheatgrass than on Indian ricegrass ( $125.7 \pm 39.3$  versus  $82.9 \pm 23.8$ ), although this difference was not statistically significant ( $t = 0.22$ ,  $df = 12$ ,  $P = 0.83$ ). By the end of the experiment, the average control plant of crested wheatgrass bore  $>1,000$  aphids, whereas the average control plant of Indian ricegrass bore  $<200$  (Fig. 1). For both hosts, final aphid densities were higher on control plants in 1996 than in 1995 (Fig. 1). This result was probably not caused by differences in ambient temperatures, which were quite similar between years (Table 3). Instead, plants were likely to have been of higher nutritional quality in 1996 because we conducted the experiment earlier in the season, and the seasonal decline in plant quality is much more pronounced for crested wheatgrass than for Indian ricegrass (Messina et al. 1993b).

Both predators were highly effective on each host in 1996, despite the relatively large sizes of aphid aggregations when predators were introduced into the cages. Aphid densities were reduced by  $>90\%$  in all 4 predator species-plant species combinations (Fig. 1). Final aphid density depended on both plant and predation treatments, but there was no plant  $\times$  predation interaction (Table 2). In contrast to the 1995 experiment, the effect of predation treatment remained significant after control plants were removed from the analysis ( $F = 6.98$ ;  $df = 1, 36$ ;  $P = 0.01$ ), because aphid densities on both grasses were lower if plants received lacewings instead of beetles (Fig. 1). The effect of host plant was only marginally significant after control plants were removed ( $F = 3.62$ ;  $df = 1, 36$ ;  $P = 0.07$ ), and the plant  $\times$  predation interaction remained nonsignificant ( $F = 0.08$ ;  $df = 1, 36$ ;  $P = 0.77$ ). Lacewings eliminated aphids from 3 of 10 crested wheatgrass plants and 4 of 10 Indian

Table 3. Mean  $\pm$  SE daily-maximum and daily-minimum temperatures ( $^{\circ}\text{C}$ ) and total precipitation (mm) during three field experiments

Experiment (dates)	$T_{\text{max}}$	$T_{\text{min}}$	Precipitation
1995—whole plants (26 July–17 Aug.)	$31.9 \pm 0.7$	$11.6 \pm 0.6$	1.5
1996—whole plants (14 June–8 July)	$30.1 \pm 0.8$	$11.4 \pm 0.7$	2.3
1996—individual culms (10 May–5 June)	$20.2 \pm 0.9$	$6.6 \pm 0.6$	96.5

Table 4. Mean  $\pm$  SE number of aphids on individual culms of 2 range grasses in the presence or absence of predators

Treatment	Crested wheatgrass	Indian ricegrass
Early harvest plants <sup>a</sup>	21.7 $\pm$ 2.2	16.5 $\pm$ 2.3
Experimental plants <sup>b</sup>		
Control	32.4 $\pm$ 4.8	25.0 $\pm$ 3.9
Lacewing larvae	1.6 $\pm$ 1.2	1.6 $\pm$ 1.0
Ladybird beetles	8.3 $\pm$ 3.3	10.8 $\pm$ 2.3

<sup>a</sup> Early harvest plants estimate aphid densities when predators were added;  $N = 6$  plants per host.

<sup>b</sup>  $N = 12$  plants per host.

ricegrass plants; beetles did not eliminate aphids from any plant.

Aphids occurred in small aggregations on isolated culms in 1996, in part because of cool temperatures and an extraordinarily high amount of rain during this field experiment (Table 3). Aphid density was higher on crested wheatgrass than on Indian ricegrass at the time predators were introduced, but not significantly so (Table 4;  $t = 1.57$ ;  $df = 10$ ,  $P = 0.15$ ). Predation treatment had a strong effect on final aphid densities, but there was no effect of host plant or any plant  $\times$  predation interaction (Table 2). Lacewing larvae again reduced mean aphid densities by  $>90\%$  on both hosts, but beetles reduced aphid populations by 74% on crested wheatgrass and by 57% on Indian ricegrass (Table 4). As a consequence, the effect of predation treatment remained significant after control plants were removed ( $F = 30.75$ ;  $df = 1, 43$ ;  $P < 0.001$ ), but the effects of host plant and the plant  $\times$  predation interaction were again nonsignificant ( $P \geq 0.20$ ). The probability of aphid extinction strongly depended on predator species; lacewing larvae eliminated aphids from 9 of 12 crested wheatgrass plants and 6 of 12 Indian ricegrass plants, whereas beetles eliminated aphids from only a single plant of each species.

**Leaf Measurements.** Greenhouse seedlings of 2 grasses did not differ in leaf length, but were strikingly different in the maximum width of an unfurled leaf and, more importantly, in the width of junction between the leaf blade and its sheath (Table 5). Sheath/blade junctions on Indian ricegrass leaves were often only as wide as 2 aphid adults; those of crested wheatgrass were both larger and more variable. The coefficient of variation for junction width was 22% for Indian ricegrass versus 40% for crested wheatgrass. As expected, the diameter of the leaf roll on field culms was considerably larger on crested wheatgrass than on Indian ricegrass (Table 5). For each grass species, the range of values of leaf-roll diameters on field culms was comparable to range of widths of leaf-sheath/leaf blade junctions on seedlings.

### Discussion

We used a series of experiments to test whether the impact of generalist predators on the Russian wheat aphid depended on grass species and, in par-

Table 5. Means  $\pm$  SE and ranges (in parentheses) of leaf dimensions (in mm) on greenhouse and field plants of crested wheatgrass and Indian ricegrass

	Crested wheatgrass	Indian ricegrass	<i>t</i>	<i>P</i>
Greenhouse plants <sup>a</sup>				
Leaf length	26.5 $\pm$ 0.8 (17.1–40.1)	25.6 $\pm$ 0.9 (16.5–40.2)	0.81	0.42
Maximum leaf width	4.5 $\pm$ 0.1 (3.2–5.6)	1.3 $\pm$ 0.03 (0.7–1.6)	22.65	$<0.001$
Width of sheath/blade junction	2.4 $\pm$ 0.2 (0.9–3.8)	1.0 $\pm$ 0.1 (0.6–1.4)	7.20	$<0.001$
Field plants <sup>b</sup>				
Culm length	50.6 $\pm$ 1.5 (41.8–58.5)	44.9 $\pm$ 2.9 (36.0–62.0)	1.86	0.08
Leaf roll diameter	2.0 $\pm$ 0.3 (0.9–3.9)	0.8 $\pm$ 0.1 (0.5–1.2)	3.35	$<0.01$

<sup>a</sup>  $n = 27$  plants per host.

<sup>b</sup>  $n = 10$  plants for crested wheatgrass, 8 for Indian ricegrass.

ticular, whether predators would be more successful in reducing aphid numbers on Indian ricegrass than on crested wheatgrass. Our results provided mixed support for these predictions. On greenhouse seedlings, both predators were more effective in reducing aphid density on Indian ricegrass than on crested wheatgrass, but the magnitude of the host-plant effect was greater for ladybird beetles than for lacewing larvae (Table 1). Given wide variation in the sizes and searching modes of predators and parasitoids, we expect that plant effects on herbivore susceptibility will commonly depend on this sort of interaction between traits of the predator and traits of the host plant. Grevstad and Klepetka (1992) observed that the effects of plant architecture on the susceptibility of cabbage aphids were similar among 5 predator species, but all predators in their study were adult coccinellids. The field experiment in 1995 provided the strongest support for increased aphid vulnerability on Indian ricegrass. Final aphid densities were significantly lower on this host (Fig. 1), and both predators eliminated aphids more frequently on Indian ricegrass than on crested wheatgrass. The effect of host plant was weaker in a similar experiment in 1996 (particularly if control plants are removed from the analysis; Fig. 1) and was negligible when predators were released on individual culms (Tables 2 and 4).

Our experiments do not allow us to attribute differences in aphid predation risk to differences in grass architecture per se; a more direct test of the effect of architecture would require the use of artificial models (Frazer and McGregor 1994, Geitzenaar and Bernays 1996) or plant lines that are isogenic at all loci except those controlling architectural traits (Kareiva and Sahakian 1990). However, detailed observations of both aphid feeding locations and predator foraging behavior support the hypothesis that leaf architecture mediates differences in aphid susceptibility on Indian ricegrass and crested wheatgrass (unpublished data). On Indian ricegrass, Russian wheat aphids are less likely

to occur within leaf rolls and are often completely exposed on the outer, abaxial surface of tightly rolled leaves. Continuous observations of individual predators have shown that generalist predators consistently contact and capture aphids at a higher frequency on Indian ricegrass than on crested wheatgrass. Thus, both short-term estimates of predation rates in the laboratory and population-level experiments in the field suggest that spatial refuges in the form of leaf rolls are more common on crested wheatgrass than on Indian ricegrass. It would be useful to obtain parallel data for susceptible and resistant varieties of cereals.

Although final aphid densities suggested that predators were sometimes more effective on crested wheatgrass than on Indian ricegrass, the probability of aphid extinction depended more on predator species than on plant species. Lacewing larvae were more effective than beetles in reducing aphid densities in 3 of the 4 experiments, but their greater effectiveness was even more apparent with regard to the probability of aphid extinction. Across the 4 experiments, aphid colonies were extinguished on 48% of plants receiving lacewings versus only 11% of those receiving beetles. The ability of a natural enemy to drive its prey to extinction may be an especially important predictor of successful biological control (cf., Hawkins et al. 1993, Myers et al. 1994). It is tempting to suggest that the smaller lacewing larvae were better able to exploit aphids within leaf rolls (Kauffman and LaRoche 1994), but we cannot exclude the possibility that differences in predator effectiveness depended on their relative densities. Because per capita consumption rates of lacewing larvae were judged to be lower than those of adult beetles, we added 2–3 times more lacewings than beetles per cage. The strongest evidence for the greater efficacy of lacewing larvae was obtained from the experiment using isolated culms (Table 4), in which the ratio of lacewings to beetles per cage was only 2:1 and both predators searched over relatively little plant material. Aphids in this experiment were eliminated from 63% of cages receiving lacewings versus only 8% of those receiving beetles. The consistent effectiveness of lacewing larvae on range grasses (Messina et al. 1995) suggests that this predator may be suitable for inundative or augmentative releases in cereals despite the tendency of *D. noxia* to feed in rolled leaves.

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#### References Cited

- Armstrong, J. S., M. R. Porter, and F. B. Peairs. 1991. Alternate hosts of the Russian wheat aphid (Homoptera: Aphididae) in northeastern Colorado. *J. Econ. Entomol.* 84: 1691–1694.
- Barbosa, P., and D. K. Letourneau. 1988. Novel aspects of insect-plant interactions. Wiley, New York.
- Burd, J. D., and R. L. Burton. 1992. Characterization of plant damage caused by Russian wheat aphid (Homoptera: Aphididae). *J. Econ. Entomol.* 85: 2017–2022.
- Carter, M. C., D. Sutherland, and A.F.G. Dixon. 1984. Plant structure and the searching efficiency of coccinellid larvae. *Oecologia (Berl.)* 63: 394–397.
- Clement, S. L., R. C. Johnson, and K. S. Pike. 1990. Field populations of the Russian wheat aphid (Homoptera: Aphididae) and other cereal aphids on cool-season perennial grass accessions. *J. Econ. Entomol.* 83: 846–849.
- Formosoh, E. S., and G. E. Wilde. 1993. Preference and development of two species of predatory coccinellids on the Russian wheat aphid and greenbug biotype E (Homoptera: Aphididae). *J. Agric. Entomol.* 10: 65–70.
- Frazer, B. D., and R. R. McGregor. 1994. Searching behaviour of adult female Coccinellidae (Coleoptera) on stem and leaf models. *Can. Entomol.* 126: 389–399.
- Geitzenauer, H. L., and E. A. Bernays. 1996. Plant effects on prey choice by a vespid wasp, *Polistes arizonensis*. *Ecol. Entomol.* 21: 227–234.
- Grevstad, F. S., and B. W. Klepetka. 1992. The influence of plant architecture on the foraging efficiencies of a suite of ladybird beetles feeding on aphids. *Oecologia (Berl.)* 92: 399–404.
- Hawkins, B. A., M. B. Thomas, and M. E. Hochberg. 1993. Refuge theory and biological control. *Science (Wash. D.C.)* 262: 1429–1432.
- Hemptonne, J.-L., A.F.G. Dixon, and G. Lognay. 1996. Searching behavior and mate recognition by males of the two-spot ladybird beetle, *Adalia bipunctata*. *Ecol. Entomol.* 21: 165–170.
- Henry, C. S., M. M. Wells, and R. J. Pupedis. 1993. Hidden taxonomic diversity within *Chrysoperla plorabunda* (Neuroptera: Chrysopidae): two new species based on courtship songs. *Ann. Entomol. Soc. Am.* 86: 1–13.
- Kareiva, P., and R. Sahakian. 1990. Tritrophic effects of a simple architectural mutation in pea plants. *Nature (Lond.)* 345: 433–434.
- Kauffman, W. C., and S. L. LaRoche. 1994. Searching activities by coccinellids on rolled wheat leaves infested by the Russian wheat aphid. *Biol. Control* 4: 290–297.
- Kindler, S. D., and T. L. Springer. 1989. Alternate hosts of Russian wheat aphid (Homoptera: Aphididae). *J. Econ. Entomol.* 82: 1358–1362.
- Marquis, R. J., and C. Whelan. 1996. Plant morphology and recruitment of the third trophic level: subtle and little-recognized defenses? *Oikos* 75: 330–334.
- Messina, F. J., T. A. Jones, and D. C. Nielson. 1993a. Seasonal variation in performance of the Russian wheat aphid (Homoptera: Aphididae) on alternate hosts. *Environ. Entomol.* 22: 1022–1030.
- 1993b. Performance of the Russian wheat aphid (Homoptera: Aphididae) on perennial range grasses: effects of previous defoliation. *Environ. Entomol.* 22: 1349–1354.
1995. Host plant affects the interaction between the Russian wheat aphid and a generalist predator, *Chrysoperla carnea*. *J. Kans. Entomol. Soc.* 68: 313–319.

- Michels, G. J., and R. V. Flanders. 1992. Larval development, aphid consumption and oviposition for five imported coccinellids at constant temperature on Russian wheat aphids and greenbugs. *Southwest. Entomol.* 17: 233-243.
- Myers, J. H., J.N.M. Smith, and J. S. Elkinton. 1994. Biological control and refuge theory. *Science* (Wash., D.C.) 265: 811.
- Obrycki, J. J., D. B. Orr, C. J. Orr, M. Wallendorf, and R. V. Flanders. 1993. Comparative developmental and reproductive biology of three populations of *Propylea quatuordecimpunctata* (Coleoptera: Coccinellidae). *Biol. Control.* 3: 27-33.
- Price, P. W. 1986. Ecological aspects of host plant resistance and biological control: interactions among three trophic levels, pp. 11-30. In D. J. Boethel and R. D. Eikenberry [eds.], *Interactions of plant resistance and parasitoids and predators of insects*. Wiley, New York.
- Stubbendieck, J., S. L. Hatch, and C. H. Butterfield. 1992. *North American range plants*, 4th ed. University of Nebraska, Lincoln.
- Tauber, C. A., and M. J. Tauber. 1987. Inheritance of seasonal cycles in *Chrysoperla* (Insecta: Neuroptera). *Genet. Res.* 49: 215-223.
- Wilkinson, L., G. Blank, and C. Gruber. 1996. *Desktop data analysis with SYSTAT*. Prentice-Hall, Englewood Cliffs, N.J.

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